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Assessing the use of mangrove pollen as a quantitative sea-level indicator on Mahé, Seychelles

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ABSTRACT: We investigated the potential of mangrove pollen from Mahé, Seychelles, to improve existing metre-scale Late Holocene sediment-based sea-level reconstructions. Mangrove species at two mangrove sites are broadly zoned according to elevation within the tidal frame. Modern pollen rain from traps deployed for 1 year generally have a poor relationship with modern vegetation, and relatively low pollen production rates. Pollen from mangrove species that live in narrow elevation zones (e.g. *Avicennia marina*) are poorly represented in modern pollen rain, while pollen from mangrove species that live across a larger elevational range (e.g. *Rhizophora mucronata*) are relatively well represented. Pollen was found in extremely low concentrations in mangrove surface and core sediments, which inhibited further study into pollen transport and preservation. The results from this modern study demonstrate that utilizing mangrove pollen would not decrease existing metre-scale vertical uncertainties in Late Holocene sea-level reconstructions in the Seychelles. We suggest that this approach may still be successful in other locations if mangrove vegetation is (i) zoned at a more extensive lateral scale and (ii) is closely associated with modern pollen rain and surface sediments, and (iii) sedimentological conditions promote the preservation of pollen in fossil sequences. © 2021 The Authors. *Journal of Quaternary Science* Published by John Wiley & Sons Ltd.

KEYWORDS: mangrove; pollen; sea level; sedimentology

Introduction

Organic coastal sedimentary deposits are important archives of palaeoenvironmental change and are widely used to understand coastline evolution and reconstruct relative sea-level (RSL) changes. In temperate and high-latitude regions, the organic sediments of salt marshes can provide high-resolution (decimetre-scale) RSL records using microfossil-based transfer functions (Gehrels, 2000; Kemp *et al.*, 2009; Barlow *et al.*, 2013). An enhanced global spread of detailed Holocene RSL reconstructions is necessary to improve our understanding of the climatic and geophysical processes influencing RSL prior to the satellite and historical eras (Horton *et al.*, 2018). However, low-latitude coastlines and their respective organic sediments are relatively under-studied compared to their temperate counterparts.

Mangroves occupy large areas of coast in low-latitude regions and occupy a similar ecological niche to salt marshes, and have therefore been used to understand Holocene RSL changes (Scholl, 1964; Horton *et al.*, 2005; Bird *et al.*, 2010; Woodroffe *et al.*, 2015; Tam *et al.*, 2018). Yet quantitative RSL reconstructions remain challenging due to the poor preservation of microfossils such as foraminifera and diatoms that are often used by transfer function approaches (Debenay *et al.*, 2004; Woodroffe *et al.*, 2005). This preservation issue has meant that many RSL and palaeoenvironmental reconstructions from mangrove sediments are derived from pollen records (Grindrod, 1985; Woodroffe *et al.*, 1985; Ellison, 2005; Urrego *et al.*, 2013). Mangrove sediments can provide conditions that are suitable for pollen preservation: anoxia and reducing conditions, low pH and high salinity (Grindrod, 1988; Phuphumirat *et al.*, 2015).

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Mangrove species are thought to have highly localized pollen dispersal (Grindrod, 1985). This is an important observation, as unlike foraminifera or diatoms which live on or within sediments, pollen does not enter sedimentary sequences autochthonously – it is transported from the mangrove plant to the sediment surface. Mangrove pollen can be transported via animals, winds, and tidal or fluvial currents before deposition, although a majority of mangrove species are pollinated via insects and birds (Tomlinson, 2016). Mangrove species zonation is considered to be controlled by the duration and frequency of tidal inundation (Crase *et al.*, 2013), which is strongly associated with elevation and salinity. Thus, mangroves with strong (elevation-controlled) zonation patterns and highly localized pollen dispersal are potential candidates for quantitative RSL reconstructions, if pollen assemblages in surface sediments accurately and precisely reflect modern vegetation.

Pollen in mangrove surface sediments has been found to broadly reflect these zonation patterns in a number of modern mangrove environments (Grindrod and Rhodes, 1984; Behling *et al.*, 2001; Mao *et al.*, 2006; Urrego *et al.*, 2009). This relationship has also led to the use of pollen assemblages for quantitative RSL reconstructions (Ellison, 1989; Engelhart *et al.*, 2007; Punwong *et al.*, 2013a), which generally yield better vertical precision (centimetre to decimetre scale) than those constructed with a more general mangrove sediment indicative range (metre-scale). However, despite detailed modern observations in mangroves, there is little information available on the exact process of the transport of mangrove pollen from tree to sedimentary deposit. Measuring modern pollen rain using pollen traps in mangroves is challenging because of the need to site traps above the level of tidal inundation and issues with high annual or seasonal rainfall that collects in and can overflow the traps (Grindrod, 1985; Behling *et al.*, 2001). Despite this difficulty, mangrove pollen

transport processes need to be further investigated to better understand pollen transport processes and to ensure that we include realistic errors when using mangrove pollen in quantitative RSL reconstructions.

Here, we test the use of mangrove pollen as a palaeo-elevation proxy in a small island, microtidal mangrove environment to determine applicability to quantitative RSL reconstructions. We investigated modern mangrove pollen from two mangroves from Seychelles in the western Indian Ocean, using a combination of field mapping, pollen traps and surface sediment samples. Previous mangrove- and coral-derived Late Holocene RSL reconstructions from Seychelles provide a framework to test whether palynological approaches can reduce vertical reconstruction uncertainties using sediments or coral alone, which are metre-scale to decimetre-scale using mangrove pollen. This would provide much more detailed insight into Late Holocene RSL changes in this region (Camoin *et al.*, 2004; Woodroffe *et al.*, 2015).

Study site

Seychelles is a dominantly granitic archipelago located in the south-west Indian Ocean (~4–11°S) (Fig. 1). Mahé, the largest of the islands, has relatively high topographic relief (up to 905 m above sea level) (Fig. 1). The tide gauge record at Point La Rue (Mahé, 1993 to present) indicates mixed semi-diurnal tides with a maximum tidal range of 2.1 m around the coast of Mahé (Admiralty Tide Tables, 2017). The adjacent terrestrial coastal plain mostly comprises a beach plateau, which is a supratidal feature of the coastal zone around Mahé and formed during the Late Holocene as sediment supplied from the fringing reef system moved onshore as RSL stabilized (Woodroffe *et al.*, 2015). Mangrove forests began to occupy areas behind the beach plateau and tombolos by 2000 years ago, areas which provided a coastal barrier and calmer hydrological conditions. Erosion of the beach plateau by rivers created further accommodation space for mangrove establishment. The vast majority of the mangrove forests behind the beach plateau have now been reclaimed as residential or agricultural land (Woodroffe *et al.*, 2015), and present-day mangrove forests are generally restricted to the later established riverine environments.

Two mangrove areas were selected for the pollen trap study: Grand Anse and Anse Boileau on the west coast of the island of Mahé (Fig. 2). Generally, mangrove forests on Mahé are characterized by five species: *Rhizophora mucronata*, *Sonneratia alba*, *Bruguiera gymnorrhiza*, *Avicennia marina* and *Lumnitzera racemosa*. Minor populations of *Xylocarpus granatum*, *Ceriops tagal* and *Nypa fruitcans* are present, as well as minor and associated mangrove species *Acrostichum aureum*, *Casuarina equisetifolia* and *Pandanas tectorius* occurring near to the terrestrial forest transition. Lowland forest on this coastal plain is dominated by *Cocos nucifera* (coconut palm), *Terminalia catappa* (sea almond), *Calophyllum inophyllum* (Takamaka) and *Mimusops* sp. The Mahé mangroves are riverine mangroves, using the ecological classification of Lugo and Snedaker (1974), and are inundated daily by tides.

Methods

Field methods

Vegetation was mapped and surveyed at a total of 188 sites (129 at Grand Anse, 59 at Anse Boileau) by recording plant species (with a trunk diameter >10 cm) within a < 2 m radius of the sample location within the mangrove zones. The non-mangrove vegetation identified was generally restricted to major species found on the beach plateau. Sample sites were selected to cover a range of geomorphological, sedimentological and plant species compositions within each of the mangrove sites. Site elevations were surveyed using a theodolite and staff, and a water level

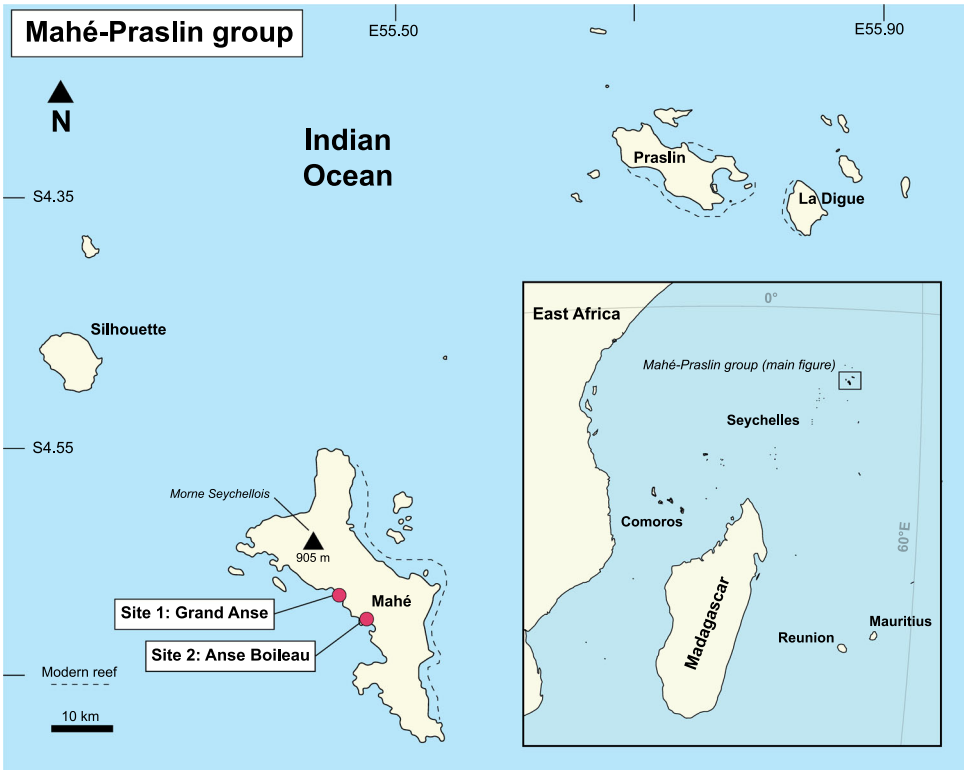

Figure 1. The Mahé-Praslin group (i.e. the granitic islands) is the northernmost island group in the Seychelles archipelago. The focus of this study is the largest and highest island, Mahé. The location of the two mangrove sites described in this study are marked. [Color figure can be viewed at wileyonlinelibrary.com]

Figure 2. (A) Pollen trap and equivalent surface sample site locations at Grand Anse mangrove area. Sample sites are coloured by mapped vegetation zones, mangrove extent is marked by the dashed white line and light blue lines are site rivers (the River Dauban). Mapped vegetation zones at each sample site are shown in the colour legend, where Bg or Bruguiera is *Bruguiera gymnorrhiza*, Am is *Avicennia marina*, Lr is *Lumnitzera racemosa*, Sa is *Sonneratia alba* and Rm is *Rhizophora mucronata*. Base map is from Google Earth (2019). (B) Pollen trap and equivalent surface sample site locations at Anse Boileau mangrove area. Sample sites are coloured by mapped vegetation zones, mangrove extent is marked by the dashed white line and light blue lines are site rivers (the River Cayman). Mapped vegetation zones at each sample site are shown in the colour legend, where Bg or Bruguiera is *Bruguiera gymnorrhiza*, Am is *Avicennia marina*, Lr is *Lumnitzera racemosa*, Sa is *Sonneratia alba* and Rm is *Rhizophora mucronata*. Base map is from Google Earth (2019). [Color figure can be viewed at wileyonlinelibrary.com]

logger was deployed to characterize the tidal timings and amplitudes at the Grand Anse mangrove for ~15 days. Data collected from the water level logger were compared to observations from the Point La Rue tide gauge (UHSLC 2019), and sample elevations were related to mean tide level (MTL) from timed water level measurements in calm-water locations in the mangrove. While there is a minor timing offset between the tide gauge measurements and the logger data (~25 min later at the west coast Grand Anse site compared to the east coast Point La Rue tide gauge), when this was corrected for, the tidal amplitudes between Grand Anse and Point La Rue are comparable and within the 0.1 m uncertainty within daily predicted tidal amplitudes (*Admiralty Tide Tables,* 2017). Given the proximity of the two sampled locations of Anse Boileau and Grand Anse (~3 km), the tidal logger data from Grand Anse are considered representative of both sites.

Pollen traps

Pollen traps were designed following previous modern pollen rain studies in mangroves (Behling *et al.*, 2001) and tropical rainforests (Jantz *et al.*, 2013). Traps were constructed from 50-ml plastic tubes (~11 cm in length, ~3 cm diameter opening), and filled with ~4 ml of liquid glycerol. The glycerol acts as a 'repository' medium for pollen entering the trap, as it is denser than the rainwater that would accumulate (and overflow) over time in the trap. Trap openings were covered with mosquito netting to prevent insects entering the trap. Importantly, to avoid tidal inundation and preserve the modern pollen rain unaffected by tidal or fluvial flow, traps were attached to plastic-coated poles inserted into the sediment and above the predicted maximum tidal inundation level. The collecting period was 1 year between July 2017 and July 2018.

A total of 33 traps were set in 2017, and 20 remained on collection in 2018. After collection samples were refrigerated at 4 °C until further laboratory processing could be undertaken. Trap samples were washed and centrifuged with deionized water to concentrate accumulated organic material. Pollen was isolated using standard laboratory methods (Moore *et al.*, 1991), including addition of one *Lycopodium* spore tablet (18583 spores per tablet), alkali digestion, sieving at 180 µm and acetolysis, and were stained before mounting on microscope slides.

Surface and core sediment samples

Surface sediment samples (top < 1 cm of sediment) from immediately underneath each pollen trap location were collected at the same time as the traps (July 2018), and stored at 4 °C until further laboratory processing could be undertaken. Pollen was isolated from mangrove sediment following standard procedures as above for the pollen trap samples, but with the inclusion of a hydrofluoric acid digestion step to remove minerogenic particles.

Surface sediment was also collected (as part of a wider study into mangrove sediments and RSL reconstructions) for grain size and total inorganic carbon (TIC) and total organic carbon (TOC) analyses. Grain size samples (0–2000 µm) were treated with excess hydrogen peroxide to oxidize organic matter. To deflocculate fine sediments, sodium hexametaphosphate was added to the samples. Samples were then sieved at 2000 µm immediately prior to analysis with a Beckman Coulter LS 13 320 Laser Diffraction Particle Size Analyser. Total carbon and TIC were measured on an Analytic Jena 3000 elemental analyser using 10 mg of powdered sample, and combusted at 1100 °C. TIC samples were acidified with 40% phosphoric acid prior to combustion. TOC concentrations were calculated by the difference between total carbon and TIC concentrations. Samples were measured alongside two certified reference materials to determine measurement uncertainty as well as sample replicates (which is <1% of reported values).

Core samples were also collected as part of a wider study into mangrove sediments and RSL reconstructions. Field and laboratory methods for these samples are presented in Supporting Information Text 1.

Pollen counting and identification

A minimum count of 200 pollen grains and fern spores was attempted for each pollen trap and surface sediment sample. However, as pollen concentrations were low (average count was 154), a number lower than 200 was used when more than two entire pollen slides per sample were required to achieve 200 counts (counts per sample available in Supporting Information Table S4a). Pollen was identified using published references (Thanikaimoni, 1987; Mao *et al.* 2006, 2012). Mangrove pollen grains were identified to species level, with the exception of *Bruguiera* and *Ceriops* species, which are not distinguishable with light microscopy and are thus grouped together (Engelhart *et al.*, 2007; Punwong *et al.*, 2013a). The most commonly occurring non-mangrove pollen grains were identified to genus or species level, but were otherwise grouped together as 'non-mangrove'. The pollen sum excludes fungal spores, and for further analysis was amalgamated into two groups: mangrove and non-mangrove pollen. Total mangrove counts were also subdivided further into three groups: major, minor and associated elements as per Mao *et al.* (2012) and Tomlinson (2016) subdivisions (Table S1). Pollen accumulation rates are likely to be unrealistic, because there was considerable variability in the condition of the mosquito nets on the traps upon collection (as the mosquito net reduces the area available for pollen to accumulate). We therefore present only pollen concentrations rather than accumulation rates to avoid any bias which might be introduced if the net covering impeded pollen accumulation. Pollen concentrations are calculated using the saturated weights of the total organic residue collected in the pollen traps (and before laboratory treatment).

Statistical analyses

To evaluate the relationship between modern vegetation and pollen trap samples, we calculated a number of indices proposed by Davis (1984): (i) the association index (*A*) which measures whether the presence of a pollen type indicates the presence of the parent plant species in the local environment; (ii) the under-representation index (*U*), which measures under-representation of pollen types when the parent plant species is present in the local environment; and (iii) the over-representation index (*O*), which measures the over-representation of pollen types where a parent plant species is absent in the local environment. These indices are calculated by the formulae:

$$A = \frac{\mathrm{B0}}{\mathrm{P0} + \mathrm{P1} + \mathrm{B0}}$$

$$U = \frac{\mathrm{P1}}{\mathrm{P1} + \mathrm{B0}}$$

$$O = \frac{\mathrm{P0}}{\mathrm{P0} + \mathrm{B0}}$$

where B_0 is the number of sites where both the pollen type and the parent plant species are present in the local environment, P_0 is the number of sites where the pollen type is present but the parent plant species is absent in the local environment, and P_1 is the number of sites where the pollen type is absent but the plant species is present in the local environment. These semi-quantitative indices are useful because the small areal extent of the Grand Anse and Anse Boileau mangroves does not permit traditional quantitative quadrat vegetation mapping, and therefore regression analysis and other quantitative models between modern vegetation and pollen trap samples cannot be undertaken (e.g. Davis, 1984; Urrego *et al.*, 2009). Other models that examine the relationship between pollen representation and vegetation are not suitable in our study area as they are developed for different depositional environments (e.g. lakes or lagoons), wind-borne pollen and large areal extents (kilometre-scale) (Sugita, 1994; Azuara *et al.*, 2019).

To determine possible ordination of pollen trap data with respect to environmental variables, we performed detrended correspondence analysis (DCA) and redundancy analysis (RDA) to test the ordination of data with respect to environmental variables (e.g. elevation, distance from open shore and sediment composition) (Engelhart *et al.*, 2007; Urrego *et al.* 2009, 2010). The analyses were performed in R (version 3.6.1) using the 'vegan' package (Oksanen, 2019).

Results

Modern vegetation

At Grand Anse, sites proximal to the river channel are generally dominated by *Sonneratia alba* and *Rhizophora*

mucronata mangroves, with *Bruguiera gymnorrhiza* and *Rhizophora mucronata* inhabiting more interior zones of the mangrove (Fig. 3). Sites in the most landward section of the Grand Anse mangrove (and generally at higher elevations) were dominated by a mix of *Avicennia marina* and *Lumnitzera racemosa*. *Acrostichum aureum* and *Casuarina equisetifolia* dominate the fringes of the mangrove zone near the terrestrial transition. At Anse Boileau (Fig. 4), vegetation zonation is generally similar to at Grand Anse, but more landward/higher elevation zones were dominated by *Avicennia marina* and *Lumnitzera racemosa* was notably absent. Residential development around the fringes of the Anse Boileau mangrove has limited the extent of the zone inhabited by *Acrostichum aureum* and *Casuarina equisetifolia* (which is present at Grand Anse).

Using this survey data from both mangrove sites, mangrove vegetation zones occupy a maximum elevation range between −0.58 to +0.82 m MTL, although different vegetation groups inhabit different elevation ranges (Fig. 5). *Avicennia marina* and *Lumnitzera racemosa* tend to occupy narrower and higher elevation ranges within the mangrove zone (between +0.21 and +0.53 m MTL at Grand Anse, and between +0.06 and +0.45 m MTL at Anse Boileau), while mixed *Sonneratia alba* and *Rhizophora mucronata* stands occupy the whole of the mangrove zone. The terrestrial-dominated vegetation zone is found above all the mangrove zones. Modern survey data are available in Supporting Information Tables S2 and S3.

Pollen trap data

Pollen trap sample abundances (of samples >5% of the pollen sum) and pollen group totals are presented along with pollen and fern spore counts in Fig. 6 (data available in Supporting Information Table S4a and S4b). Only 10 samples out of 20 pollen trap samples reached the required pollen sum of 200 grains, with five samples reaching only 50 grains from two pollen slides. Pollen traps contain pollen and fern spores from five major mangrove species, and considerable abundances of *Casuarina equisetifolia* and *Acrostichum aureum*. Total non-mangrove pollen varies from ~6 to 57% abundance in the pollen trap samples, of which *Cocos nucifera* and *Terminalia catappa* are dominant species. At Grand Anse, major mangrove species abundance generally reduces with increasing elevation, while minor and associated mangrove species abundance generally increases with increasing elevation. This pattern is not as evident in the Anse Boileau pollen trap data.

Pollen concentrations vary greatly between mapped vegetation zones (Table 1). Terrestrial-dominated and mixed *Sonneratia alba* and *Rhizophora mucronata* vegetation zones have pollen concentrations an order of magnitude greater than all other vegetation zones. Averaged pollen trap concentration from Grand Anse is also higher than that of Anse Boileau.

The *A* (association), *O* (over-representation) and *U* (under-representation) indices are presented in Table 2. *Rhizophora mucronata* is the only major species with a high association index (i.e. $A \geq 0.5$). Although *Pandanas tectorious* and *Lumnitzera racemosa* also have high association indices ($A = 1.00$), these values are calculated from only one sample in both cases. *Avicennia marina* and *Bruguiera/Ceriops* species have intermediate values ($A = \sim 0.3$) which suggests there is still a reasonably close association between species presence and pollen occurrence. *Sonneratia alba*, *Casuarina equisetifolia* and *Acrostichum aureum* have low values ($A < 0.2$), which indicates that the presence of pollen has a low association with the presence of the parent plant species.

High over-representation indices can indicate either high or low pollen production rates. *Casuarina equisetifolia* and *Acrostichum aureum* have high *O* index values, probably indicating high pollen production rates, because their pollen abundances in pollen trap samples are relatively high (i.e. high $\bar{X}_p$ values). The majority of other species also have high *O* index values (e.g. *Sonneratia alba*) but these are more likely to be low pollen producers as pollen abundances in pollen trap samples are relatively low. *Avicennia marina* and *Sonneratia alba* have high under-representation indices ($U = 0.5$ and 0.67, respectively), and *Bruguiera/Ceriops* has intermediate values ($U = 0.43$). These three species/groups have concurrently high *O* index values, which suggests they have low

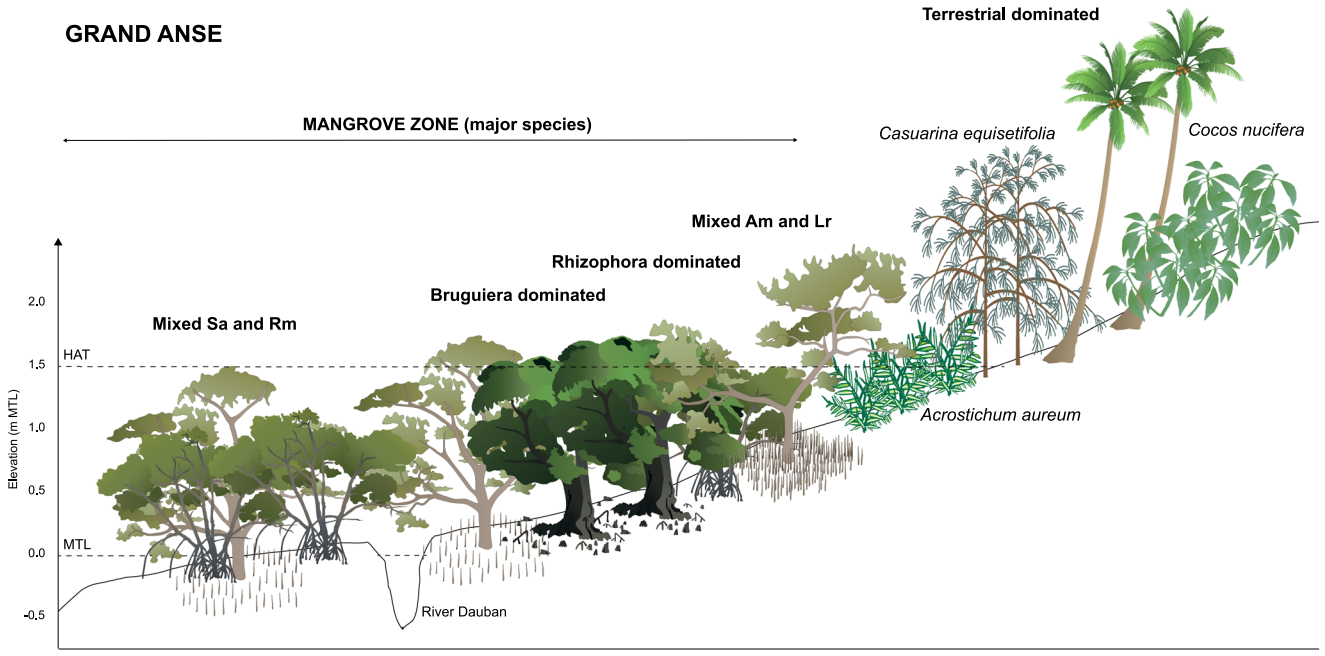

Figure 3. Schematic diagram of the surveyed vegetation zones at the Grand Anse mangrove. The overall mangrove zone includes the major species as per the Mao *et al.* (2012) classification. The zones relate qualitatively to the zones displayed in Fig. 6. Vegetation key: Sa is *Sonneratia alba*, Rm is *Rhizophora mucronata*, Am is *Avicennia marina* and Lr is *Lumnitzera racemosa*. Mangrove symbols are courtesy of the Integration and Application Network (ian.umces.edu/symbols/), University of Maryland Center for Environmental Science. [Color figure can be viewed at wileyonlinelibrary.com]

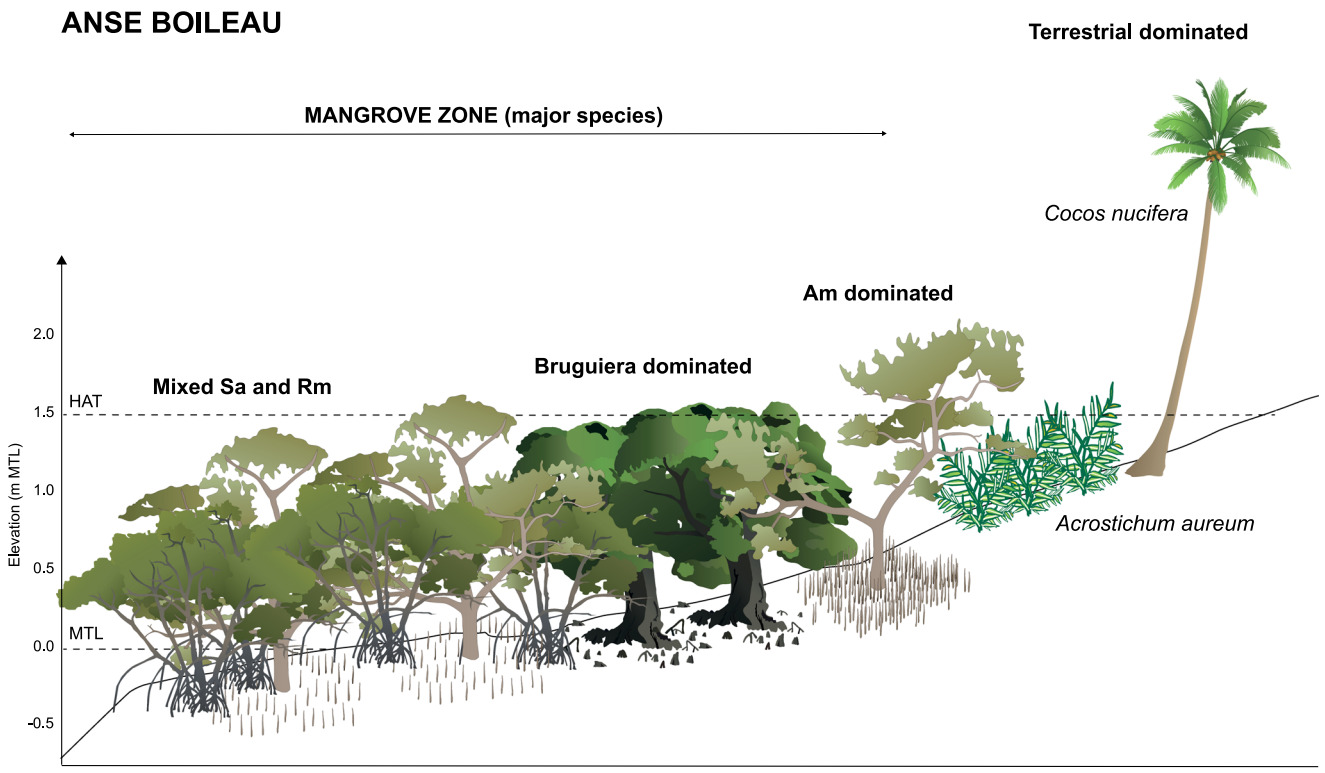

Figure 4. Schematic diagram of the surveyed vegetation zones at the Anse Boileau mangrove. The overall mangrove zone includes the major species as per the Mao *et al.* (2012) classification. The zones relate qualitatively to the zones displayed in Fig. 6. Vegetation key: Sa is *Sonneratia alba*, Rm is *Rhizophora mucronata*, Am is *Avicennia marina*. Mangrove symbols are courtesy of the Integration and Application Network (ian.umces.edu/symbols/), University of Maryland Center for Environmental Science. [Color figure can be viewed at wileyonlinelibrary.com]

pollen production rates but have relatively efficient pollen dispersal mechanisms; that is, a species may produce relatively low amounts of pollen but it can travel relatively far from its source. Species with low *U* index values and high *O* index values (e.g. *Nypa fruticans*) indicate low pollen production and/or less efficient dispersal mechanisms.

Surface and core sediment data

Surface sediment samples contained very low abundances of pollen (e.g. typically five sample pollen, and similar number of *Lycopodium* marker pollen per microscope slide). Counts were so low that we decided that it was not practical to undertake any further palynological analyses on the surface sediment samples as part of this study.

The surface sediments at Grand Anse and Anse Boileau sites are typically sand-sized, varying from dominantly well-sorted medium sand (~200 µm on average) to coarse, poorly sorted sand >500 µm (Supporting Information Table S5). Silt and clay-sized particles make up lesser proportions of the otal sediment grain size, but Anse Boileau samples have generally higher amounts of silt and clay than Grand Anse. At Grand Anse, TOC is 0.9–22% and TIC is 0–10.8%. TOC at Anse Boileau is 4.5–18.6% and TIC is 0–4.7% (Table S5). Core sediment samples contained very low pollen abundances similar to that reported for surface sediments.

Statistical analyses

To determine whether the pollen trap dataset is more suited to linear or unimodal ordination methods, we log-transformed the dataset and performed DCA on selected species that have a total abundance of >5% (Fig. 7). The length of the first DCA axis is <4, which suggests linear ordination methods are more appropriate for the pollen dataset. We then performed RDA using the log-transformed pollen dataset and the environmental variables (elevation, distance from shore, vegetation zone, grain size and TOC/TIC%). The RDA model shows the proportion of constrained inertia (variance explained by the environmental variables) is 50.1%. The associated Monte Carlo permutation test suggests that the variance explained by the environmental variables is not significant ($p = 0.09$, 999 permutations). To explore this further we separated the environmental variables into three groups and performed separate RDA models: spatial variables (elevation, distance from shore and vegetation zone), grain size variables (fine sand, coarse sand, silt and clay) and composition (TOC and TIC). The variance explained by these three separated groups was significant, with p values of 0.026, 0.006 and 0.038 respectively. Further analysis of each group of variables using the variation partitioning method yielded low adjusted R^2 values (i.e. low levels of explained variance, all <0.11) and p values of >0.05 for individual and shared variance explained by the environmental variables (Supporting Information Table S6). We suspect that the small lateral extent and compressed environmental gradients at both mangrove sites has an effect on the ability of mangrove plant communities to develop clear elevation zonation, which is reflected in the low DCA axis 1 score and the results of the subsequent RDA (Fig. 7). While we can qualitatively suggest that elevation appears to play some role in determining the distribution of modern mangrove pollen rain at our sites, we cannot confidently quantify this.

Discussion

Pollen as a sea-level indicator in Seychelles mangrove sediments

The results derived from the pollen traps and very low amounts of surface sediment pollen found in our samples do not provide sufficient justification for the use of pollen to improve the resolution of quantitative RSL reconstructions in Seychelles

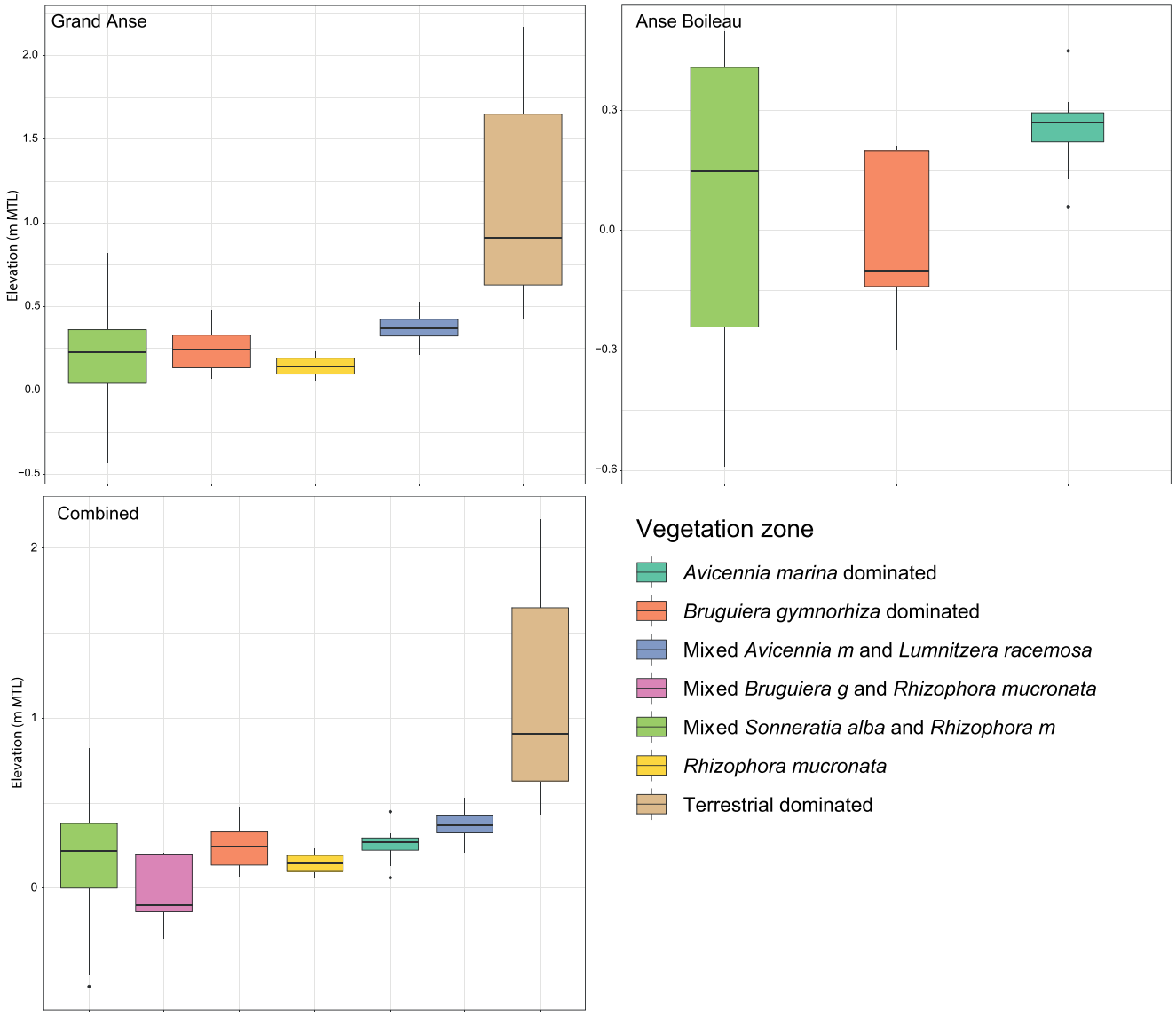

Figure 5. Box and whisker plot of mangrove vegetation zones surveyed from Grand Anse ($n = 129$), Anse Boileau ($n = 59$) and combined datasets ($n = 188$). The terrestrial-dominated zone mapped here includes *Casuarina equisetifolia*, which although being classed as a minor mangrove species, occurs at the upper edges of the mangrove zone along with other non-mangrove species. [Color figure can be viewed at wileyonlinelibrary.com]

mangrove sediments. While modern vegetation survey and pollen trap data do show a relationship with elevation (Figs. 5 and 7), the pollen trap association and representation indices indicate that pollen rain does not necessarily reflect species abundance across the mangrove zone. This is also reflected in the RDA where vegetation zone appears to be less important in determining variance in the pollen trap data than other environmental variables (e.g. distance from shore, grain size). *Rhizophora mucronata* pollen is closely associated with the presence and abundance of its parent plant (Table 2), and this species has relatively higher levels of pollen production and efficient dispersal; this observation is consistent with other mangroves worldwide (Behling *et al.*, 2001; Engelhart *et al.*, 2007; Urrego *et al.* 2009, 2010). In Seychelles, *Rhizophora mucronata* lives over the largest elevation range of all species in the mangrove zone (Fig. 5). Species that live in the narrowest elevation ranges in the mangrove zone (e.g. *Avicennia marina* and *Lumnitzera racemosa*) have relatively low pollen production and therefore very low average percentages. A plant of this type can be a dominant species within any specific mangrove zone, but may at the same time be poorly represented or entirely absent in pollen trap samples. This characteristic makes it difficult to interpret whether the presence or absence of these pollen species indicates the presence or absence of the parent plant.

Poor plant–pollen associations of key elevation-limited species such as *Avicennia marina* means that it is unlikely pollen can improve upon the vertical resolution of using the upper and lower limits of mangrove vegetation as an indicative meaning for Seychelles coastal sediments. Despite this, the abundance of major mangrove species decreases with increasing elevation (Fig. 6), and the abundance of minor and associated mangrove species (e.g. *Casuarina equisetifolia*) increases. While this apparent elevation relationship is clear, the RDA results suggest that many of the environmental variables are collinearly related (i.e. the variance is conditional on each other) and therefore we cannot be confident that elevation is the most dominant driver of species (and pollen) responses (Fig. 7). Rather, pollen trap assemblages appear to reflect variability associated with geomorphological factors such as distance from open shore and sediment composition, in particular TOC and TIC. Although patterns of modern mangrove vegetation appear to be related to elevation along with other environmental variables (Fig. 5), this relationship becomes more complicated when we analyse the pollen trap data, probably

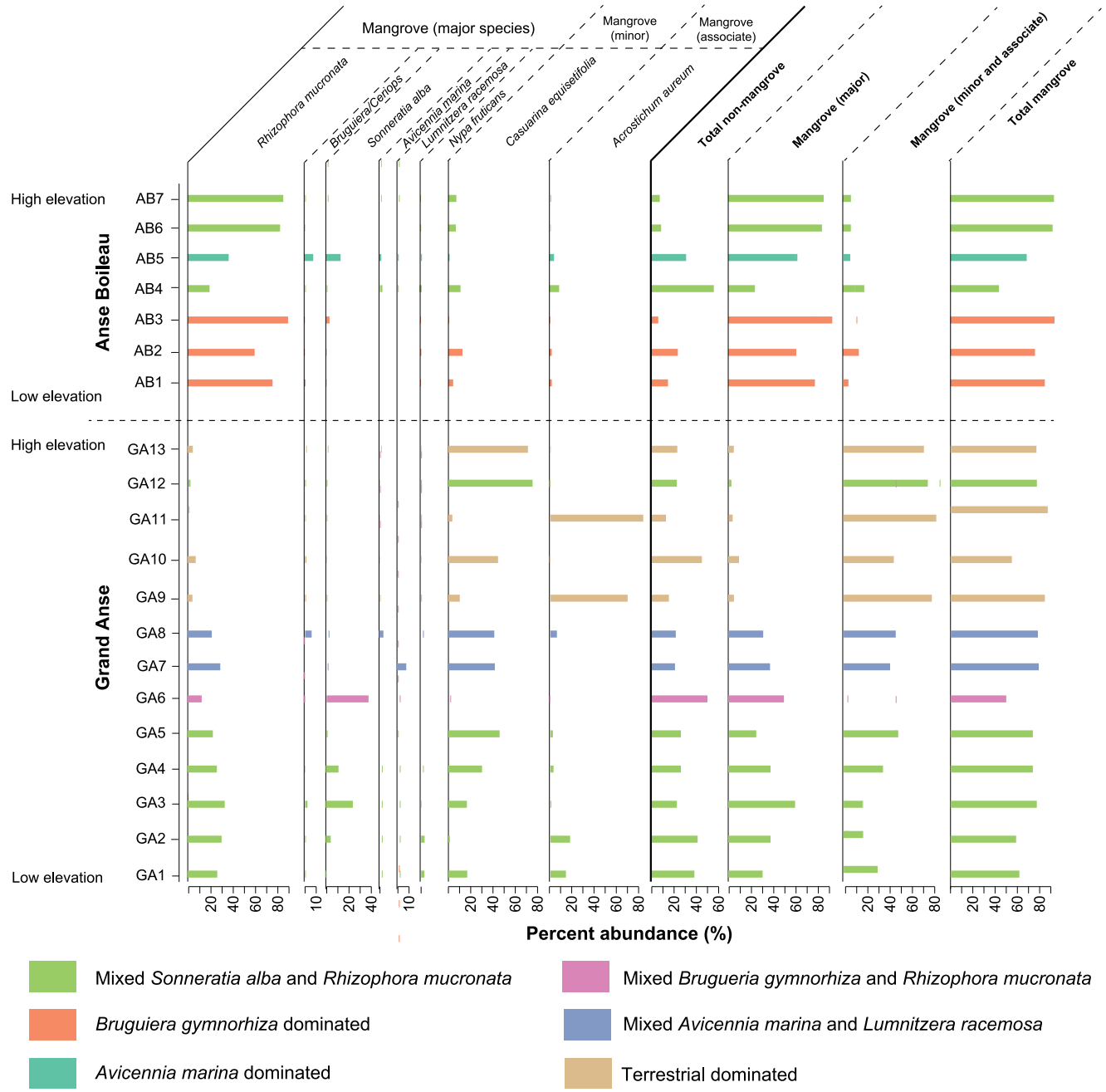

Figure 6. Pollen percentages separated by site locality. Samples are ordered by elevation. Grouping of mangrove species is consistent with categories in Mao *et al.* (2012) (Supporting Information Table S1). [Color figure can be viewed at wileyonlinelibrary.com]

Table 1. Average pollen concentrations by mapped vegetation zone. See concentration formula in Supporting Information Table S4b. The pollen concentration values are expressed as 'per year' from the 1-year experiment.

Mapped vegetation zone	Average pollen concentration (grains g^{-1} a^{-1})
Terrestrial dominated ($n = 4$)	65 487
Mixed Sa and Rm ($n = 9$)	67 425
Mixed Bg and Rm ($n = 4$)	9879
Am dominated ($n = 1$)	1950
Mixed Am and Lr ($n = 2$)	5606
Grand Anse average ($n = 13$)	63 614
Anse Boileau average ($n = 7$)	19 908

Sa: Sonneratia alba; Rm: Rhizophora mucronata; Bg: Bruguiera gymnorrhiza; Am: Avicennia marina; Lr; Lumnitzera racemosa.

because of the different pollen production rates and dispersal mechanisms between mangrove species.

It is possible that in mangroves with a small present-day extent such as those at the studied sites in Seychelles, local hydro-geomorphological processes drive vegetation patterns, which are then complicated by variable pollen production and dispersal, making the use of pollen as a quantitative proxy challenging. Mangrove pollen is normally seen as a useful RSL proxy because of its highly localized dispersal (Grindrod, 1985; Ellison, 1989), but this study shows that in the setting of Seychelles this is an overly simplistic picture. In Seychelles, the presence of pollen in a sediment sequence may only be useful in distinguishing a mangrove depositional environment from other organic sediments (e.g. a freshwater wetland or salt marsh) that may otherwise be difficult to distinguish based on sedimentology and visual description alone. While there are very few areas of freshwater wetlands and no salt marshes in Seychelles to test this hypothesis, this may be a useful

Table 2. Association (*A*), over-representation (*O*) and under-representation (*U*) indices (Davis, 1984) for major, minor and associated mangrove species found in pollen trap sites at Grand Anse and Anse Boileau. B_0 is the number of samples where both plant species and pollen type are present at a sample site, P_0 is the number of samples where a plant species is absent but pollen type is present at a sample site, and P_1 is the number of samples where a plant species is present but pollen type is absent. See main text for formulae. *n* is the number of sample sites used to determine indices. Additionally, as per Davis (1984), $\bar{X}_p$ (*n*) is the average pollen percentages in a sample where parent plants are present (*n* = the number of samples in average calculation), and $\bar{X}_a$ (*n*) is the average pollen percentages in a sample when parent plants are absent (*n* = number of samples in average calculation).

Species	B_0	P_0	P_1	*A*	*O*	*U*	*n*	$\bar{X}_p$ (*n*)	$\bar{X}_a$ (*n*)
Rhizophora mucronata	12	8	0	0.6	0.40	0.00	20	51.8 (11)	11.1 (9)
Bruguiera/Ceriops	4	5	3	0.33	0.56	0.43	12	1.7 (6)	0.8 (14)
Sonneratia alba	1	8	2	0.09	0.89	0.67	11	8.1 (3)	4.2 (17)
Avicennia marina	3	4	3	0.30	0.57	0.50	10	1.3 (5)	0.2 (15)
Lumnitzera racemosa	1	0	0	1.00	0.00	0.00	1	8.3 (1)	0.0 (19)
Xylocarpus granatum	0	2	0	0.00	1.00	0.00	2	0 (0)	0.1 (20)
Heritiera littoralis	0	2	0	0.00	1.00	0.00	2	0 (0)	0.1 (20)
Acrostichum aureum	2	12	0	0.14	0.86	0.00	14	76.3 (2)	3.4 (18)
Nypa fruticans	1	7	0	0.13	0.88	0.00	8	0.4 (1)	0.6 (19)
Casuarina equisetifolia	1	17	0	0.06	0.94	0.00	18	71.4 (1)	19.5 (19)
Pluchea indica	0	2	0	0.00	1.00	0.00	2	0 (0)	0.1 (20)
Aegiceras corniculatum	0	1	0	0.00	1.00	0.00	1	0 (0)	0.1 (20)
Pandanas tectorious	1	0	0	1.00	0.00	0.00	1	0.8 (1)	0.2 (19)

technique to identify mangrove deposits in other small island, microtidal sites and should be tested by observing modern pollen rain across the transition between freshwater and mangrove environments.

The pollen trap data from Seychelles mangroves (in the absence of comparative surface sediment data) are in contrast with other studies that have used surface sediment pollen assemblages to justify the use of pollen for quantitative RSL and/or palaeoenvironmental reconstructions. Engelhart *et al.* (2007) and (Punwong *et al.*, (2013a, 2013b) working in extensive mangrove stands in Indonesia and Tanzania found a good association of plant presence with pollen presence in surface sediment. This enabled the use of pollen assemblages to quantitatively reconstruct elevations and improve the vertical resolution of RSL reconstructions. However, Seychelles mangrove sites differ from those of the above studies in that they: (i) are much smaller in lateral extent and therefore have less developed and extensive mangrove zonation and/or (ii) are less connected to the open shoreline and are more dominated by riverine processes and sedimentation. Another key difference between these studies and the Seychelles sites is that the presence of *Avicennia* pollen species appears to be better associated with the presence of parent plants than we find in this study. A high *Avicennia* pollen–plant association has also been found in other surface sediment and pollen trap studies in Brazil, New Zealand and Colombia (Behling *et al.*, 2001; Deng *et al.*, 2006; Urrego *et al.*, 2010). It is possible that if the pollen monitoring was conducted over several years (rather than only one as in this study) the traps would have been able to capture multi-year mangrove flowering cycles (Tomlinson, 2016). It is also possible that had sufficient numbers of pollen been detected in surface sediment samples, there could have been a better plant–pollen association as surface sediment is considered to provide a multi-year pollen flux average (Engelhart *et al.*, 2007).

Preservation of pollen in mangrove sediments

Despite the relatively good preservation of pollen in pollen trap samples, an assessment of the transport of pollen from tree to sediment surface was not possible as part of this study due to the lack of pollen detected in the Grand Anse and Anse Boileau surface sediment samples. These extremely low pollen counts suggest either: (i) the laboratory process did not sufficiently isolate pollen grains for light microscopy analysis or (ii) pollen has been degraded or transported by post-depositional processes. We followed standard pollen isolation procedures (Moore *et al.*, 1991), which have been used extensively in other mangrove settings, although counts were low for both *Lycopodium* marker pollen and for sample pollen. This suggests the pollen residues contain too much organic material that was not removed during chemical and physical processing, which meant that it was not possible to find enough marker and sample pollen within a practical time limit per sample. Other pollen isolation procedures use heavy-liquid separation rather than chemical dissolution (Campbell *et al.*, 2016). A heavy-liquid separation method we used on sediment cores collected from Grand Anse (as part of a wider RSL study) yielded very low pollen abundances (see Supporting Information Text 1), but we cannot rule out that an additional different processing method may yield different results.

Low pollen concentrations have been reported in other mangrove sediment studies where multiple microscope slides were needed to obtain statistically robust counts from both surface and fossil sediment samples (Behling *et al.*, 2004; Engelhart, 2007; Punwong, 2013). However, other studies on mangrove sediments report high concentrations (>30 000 grains per gram of sediment) and abundance of mangrove pollen (>80%) across different sedimentological settings (Ellison and Strickland, 2015; Ellison, 2019). The small extent of the Seychelles mangroves, low pollen production and/or other sedimentological processes may have led to decreased preservation of mangrove pollen at our study site compared with other sites.

Pollen is one of the most widely used palaeoenvironmental proxies in mangrove sediments, largely due to the prevailing sediment conditions that enhance pollen preservation. However, when certain sediment conditions are not met, pollen grains can be degraded post-deposition. Coarser grained sediments (sand-sized and larger) have greater interstitial pore space that can be filled by incoming tidal or river waters, which can abrade pollen grains (Fægri, 1971; Grindrod, 1988). Similarly, greater interstitial pore space allows oxidation of pollen grains to occur when sediments are not inundated and/or saturated (Grindrod, 1988). The wetting and drying of mangrove sediments with tidal inundation and seasonal rainfall patterns can expand and contract pollen grain walls, which can weaken pollen grains over time (Campbell and

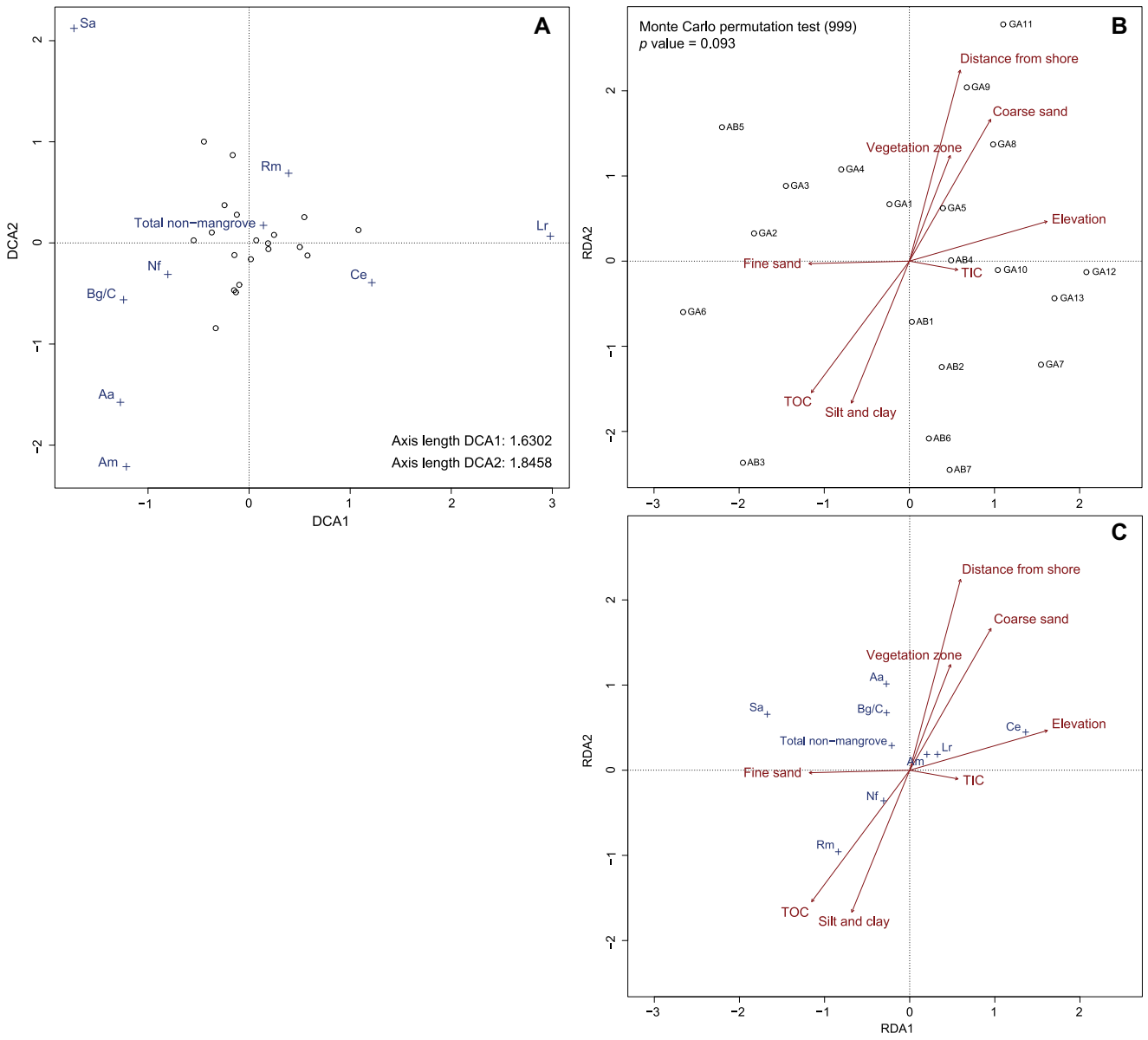

Figure 7. (A) DCA scores for pollen trap assemblage data: species coordinates are crosses and sample coordinates are circles. (B) RDA for pollen trap dataset with measured environmental variable eigenvectors, with sample site coordinates plotted as circles. (C) as for B but species coordinates plotted instead of site scores. Variables included in the analysis are elevation (m MTL), distance from shore (m), vegetation zone (1–5, see Supporting Information Table S2), grain size (coarse sand is 500–1000 μm, fine sand is 63–250 μm, silt and clay is <63 μm), and TOC/TIC (%). Species codes are Rm (*Rhizophora mucronata*), Sa (*Sonneratia alba*), Bg/C (*Bruguiera gymnorhiza/Ceriops* sp.), Aa (*Acrostichum aureum*), Nf (*Nypa fruticans*), Am (*Avicennia marina*), Lr (*Lumnitzera racemosa*) and Ce (*Casuarina equisetifolia*). [Color figure can be viewed at wileyonlinelibrary.com]

Campbell, 1994). Variable salinity conditions in sediments over time due to seasonal rainfall and river discharge may also affect the preservation of pollen grains (Campbell and Campbell, 1994). In an experimental study, Phuphumirat *et al.* (2015) found that pollen degradation rates in mangrove sediments in Thailand were lessened in fine-grained sediments that were saturated and/or inundated for greater time periods. Phuphumirat *et al.* (2015) also found that pollen degradation was enhanced in sediments with relatively low salinity and less acidic conditions. Bacterial and fungal activity can also degrade pollen grains (Phuphumirat *et al.*, 2011).

One or many of the processes suggested above could have resulted in post-depositional degradation of pollen grains at Grand Anse and Anse Boileau, creating the situation of extremely poor pollen preservation in surface sediments that we found in this study. The mangrove sediments at both Grand Anse and Anse Boileau are relatively coarse-grained, characterised by high percentages of coarse sands and gravels likely deposited by fluvial processes. The greater interstitial space in coarser sediments may lead to progressive abrasion of pollen grains through tidal and river pumping and/or oxidation over time, leaving very low concentrations in surface and fossil sediments to utilize for RSL or palaeoenvironmental reconstructions. Measured salinities of surface waters at Grand Anse varied from freshwater to marine levels within daily tidal inundation cycles, and thus probably with seasonal rainfall patterns (wet and dry seasons associated with the shift of the Intertropical Convergence Zone). These highly variable salinity conditions in the mangrove sediments at Grand Anse and Anse Boileau may also impact the preservation of pollen grains. Other factors that also apply to sediment organic matter in general may have led to loss of pollen grains in surface sediments. Bioturbation by crabs and mangrove roots can increase oxidation levels, and combined with low sedimentation rates and limited sediment accommodation space seen in the Seychelles mangroves further reduces the preservation potential of pollen grains. Degradation by microbial activity may have also led to loss of pollen grains in the Grand Anse

and Anse Boileau surface sediments, as evidence of such microbial attack on organic matter was observed in the core samples under light microscopy.

Conclusions

We find that mangrove pollen concentrations in surface and core sediments in Mahé, Seychelles, are extremely low in comparison with other mangroves (Ellison, 2019). While modern vegetation zonation is broadly related to elevation, there is a poor relationship between plant distribution and pollen distribution in traps and surface sediment samples. *Avicennia marina* and *Lumnitzera racemosa* occupy the smallest vertical ranges at the study sites, but these species have low pollen production levels and the pollen trap data do not reflect their modern distribution.

Very low pollen concentrations are detected in surface and shallow core sediments, preventing the assessment of pollen transport mechanisms to surface sediments or their use in fossil sediment sequences. These results suggest that the Seychelles mangroves, with their small lateral extent and narrow connections to open marine environments (<30 m), are not suitable for pollen-based quantitative RSL reconstructions. This is despite the fact that the quiet water environment of Seychelles mangroves might be initially seen as an ideal setting for zoned mangrove pollen accumulation and preservation. Sediment grain size, variable sediment saturation levels and low sedimentation rates may contribute to degradation of pollen post-deposition leading to very low pollen preservation. Despite these problems we found there were increased abundances of mangrove pollen within the mangrove zone compared to the terrestrial zone above and therefore the dominance of mangrove pollen in sediment samples is indicative of a mangrove depositional environment. Mangrove pollen abundances can therefore aid environmental interpretation where the depositional environment may be unclear from sedimentological descriptions (e.g. mangrove vs. freshwater peat).

Palynological approaches are not able to provide suitable improvements to existing vertical uncertainties on RSL reconstructions from Seychelles mangroves. This study suggests that it is unlikely that using pollen as a quantitative sea-level indicator will improve reconstructions in other small island mangroves with similar geomorphology and sediment characteristics to Seychelles. However, pollen may still be a useful quantitative sea-level indicator at other mangrove sites where: (i) mangrove vegetation and pollen zonation is more laterally extensive and is clearly distributed according to elevation, (ii) there is a good plant–pollen association, and (iii) sedimentological conditions allow for the preservation of pollen in sedimentary sequences (e.g. anoxic).

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Supporting information

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Table S1. Mangrove groupings as per Mao *et al.* (2012) that are present in the studied mangrove sites and pollen trap samples.

Table S2. Grand Anse vegetation survey data. Vegetation key: Sa is *Sonneratia alba*, Rm is *Rhizophora mucronata*, Bg is *Bruguiera gymnorhiza*, Am is *Avicennia marina*, Lr is *Lumnitzera racemosa*, Ct is *Ceriops tagal*, Aa is *Acrostichum aureum*, Nf is *Nypa fruticans*, Cn is *Cocos nucifera*, Tp is *Thespesia populnea*, St is *Scaveola taccada*, Ce is *Casuarina equisetifolia* and Pt is *Pandanas tectorius*. Vegetation zones were qualitatively assigned in the field.

Table S3. Anse Boileau vegetation survey data. Vegetation key: Sa is *Sonneratia alba*, Rm is *Rhizophora mucronata*, Bg is *Bruguiera gymnorhiza* and Am is *Avicennia marina*. Vegetation zones were qualitatively assigned in the field.

Table S4a. Grand Anse and Anse Boileau pollen trap data (raw count data). Rm is *Rhizophora mucronata*, B/C is group *Bruguiera* sp. and *Ceriops* sp., Sa is *Sonneratia alba*, Am is *Avicennia marina*, Lr is *Lumnitzera racemosa*, Aa is *Acrostichum aureum* and Ce is *Casuarina equisetifolia*. Mangrove species groupings are according to Mao *et al.* (2012) shown in Table S1.

Table S4b. Grand Anse and Anse Boileau pollen trap data (percentage total counts for species >5% pollen sum used for analysis). Rm is *Rhizophora mucronata*, B/C is group *Bruguiera* sp. and *Ceriops* sp., Sa is *Sonneratia alba*, Am is *Avicennia marina*, Lr is *Lumnitzera racemosa*, Aa is *Acrostichum aureum* and Ce is *Casuarina equisetifolia*. Mangrove species groupings are according to Mao *et al.* (2012) shown in Table S1. Pollen concentrations were calculated according to:

$$Concentration = \left(\frac{Taxa\ counts}{Lycopodium\ counts}\right) \times Total\ Lycopodium\ grains = \frac{added\,(18, 583)}{Weight\ of\ sample\,(grams)}$$

Table S5. Surface sediment sample data for pollen trap sites at Grand Anse and Anse Boileau (see Fig. 3). Fine sand is 63–250 µm, coarse sand is 500–1000 µm, silt and clay is <63 µm.

Table S6. Results of the RDA and variation partitioning analyses.

Supplementary Text 1

Data availability statement

All data associated with this study are available as part of the Supporting Information or as figures/tables.

Abbrevations. DCA, detrended correspondence analysis; MTL, mean tide level; RDA, redundancy analysis; RSL, relative sea level; TIC, total inorganic carbon; TOC, total organic carbon.

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